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A new species of wood lizard (Hoplocercinae, *Enyalioides*) from the Río Huallaga Basin in Central Peru

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Abstract

We report the discovery of a new species of *Enyalioides* from the premontane forest of the Río Huallaga basin in central Peru. The most similar and phylogenetically related species are *E. binzayedi* and *E. rudolfarndti*. However, the new species differs from *E. binzayedi* (state of character in parentheses) by having dorsal scales strongly keeled on paravertebral region and feebly keeled or smooth elsewhere (prominent medial keel on each dorsal scale), more dorsals in transverse row between dorsolateral crests at midbody 26–39, $\bar{x}$ = 30.44 (22–31, $\bar{x}$ = 27.57), and a conspicuous posteromedial black patch in the gular region of males (absent). Contrarily, adult males of the new species and *E. rudolfarndti* are readily distinguished by having a conspicuous posteromedial black patch in the gular region, absent in *E. rudolfarndti*, and by lacking a conspicuous orange blotch (faint if present) on the antehumeral region, as in *E. rudolfarndti*. We also present an updated molecular phylogenetic tree of hoplocercines, which strongly supports both referral of the newly discovered species to *Enyalioides* and its status as distinct from those recognized previously.

Key Words

Andes, *Enyalioides*, Hoplocercinae, Huallaga River, new species, Peru, phylogeny

Introduction

The Huallaga drainage flows north from the Cordillera Oriental of central Peru and has an extension of 1,138 km (SNE 2001), which makes it the largest tributary of the Marañon river. This basin harbours a great variety of ecosystems, including the Yugas, which are considered a shelter of endemic birds (Parker and O'neil 1976), mammals (Pacheco 2002) and amphibians (Lehr et al. 2002; Duellman et al. 2004). However, our knowledge on their biodiversity remains poor because the biological assessments in this area were disrupted in the eighties due to an internal war against terrorist legions and drug traffickers. Additionally, habitat destruction by coca plantations during the eighties and nineties caused dramatic forest fragmentation below 2,000 m (ONUDD 2006). Thus, it is not surprising that herpetological surveys along the Huallaga river basin in recent years have resulted in the discovery of eight new species of anurans including two species of *Gastrotheca* (Duellman et al. 2004), one of *Nymphargus* (Guayasamin et al. 2006), four of *Phrynopus* (Lehr et al. 2002; Lehr and Oroz 2012), and one of *Pristimantis* (Chávez and Catenazzi 2016), as well as five new species of lizards including one of *Euspondylus* (Chávez et al. 2017), one *Petracola* (Köhler and Lehr 2004), two *Proctoporus* (Köhler and Lehr 2004), and one *Stenocercus* (Venegas et al. 2013a).

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In an effort to improve our knowledge on the herpetofauna of the Huallaga river basin, we carried out field surveys between 2011 and 2018, which led to the discovery of a new species of wood lizard described in this paper. Among hoplocercine lizards, wood lizards (*Enyalioides*) represent one of the South American lizard groups with the highest species discovery rate (corrected for clade size) of this century. Our discovery increases to 16 the number of known species of *Enyalioides*, of which only seven were known in previous centuries.

Methods

Field techniques

Most lizards were captured by hand during night. Coordinates and elevation were taken with a GPS (Garmin, WGS84). After the specimens were euthanized with T61 (Intervet), we took muscle tissue samples from the left thigh, and stored them in cryogenic vials (Axygen) at 96% ethanol. All collected specimens were fixed in 10% formalin for 48 hours and permanently stored in 70% ethanol. Voucher specimens were deposited at the herpetological collection of the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru. Specimens were collected with the following permits: RD 0083-2011-AG-DGFFS-DGEFFS, RD 0330-2013-MINAGRI-DGFFS-DGEFFS, RD 066-2014-SERFOR-DGGSPFFS, RD 019-2015-SERFOR-DGGSPFFS, and RD 0083-2015-SERFOR-DGGSPFFS.

Morphological data

Snout-vent length (SVL) and tail length (TL) were measured with a ruler and recorded to the nearest millimeter. All other measurements (i.e., head width, length and height; rostral and mental width and height) were made with digital calipers and recorded to the nearest 0.1 mm. Sex was determined by noting the presence of hemipenes or sexually dichromatic characters. We followed the format of Torres-Carvajal et al. (2011) for the descriptions of the new species, as well as the terminology for scutellational characters and measurements. Specimens of other species of *Enyalioides* examined in this study are listed in the Suppl. material 1: Material examined. Institutional abbreviations correspond to CORBIDI, Lima, Peru; Museo de Historia Natural San Marcos (MUSM), Lima, Peru; and Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador.

DNA sequence data

Following laboratory protocols similar to those presented by Torres-Carvajal and de Queiroz (2009), we sequenced a continuous fragment of mitochondrial DNA (mtDNA) that extends from the gene encoding subunit I of the protein NADH dehydrogenase (ND1) through the genes encoding $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, subunit II of NADH dehydrogenase (ND2), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, the origin of light-strand replication (OL), $tRNA^{Cys}$, $tRNA^{Tyr}$, to the gene encoding subunit I of the protein cytochrome c oxidase (COI). We added four new sequences (GenBank accession numbers MZ130605–MZ130608) from the new species described herein to the mtDNA dataset of Torres-Carvajal et al. (2015). Our final dataset had 1,772 aligned nucleotides and 42 terminals representing 19 species of hoplocercine lizards and the outgroup taxa *Basiliscus plumifrons*, *Leiocephalus carinatus*, *Liolaemus pictus*, *Oplurus cuvieri*, and *Phrynosoma mcallii* (Torres-Carvajal and de Queiroz 2009).

Phylogenetic analysis

Editing, assembly, and alignment of sequences were performed with Geneious v9.1.8 (Kearse et al. 2012) under default settings for MAFFT (Katoh and Standley 2013). Genes were combined into a single dataset with four partitions, three corresponding to each codon position in protein coding genes and one to all tRNAs. The best partition strategy along with the corresponding models of evolution were obtained in PartitionFinder v2 (Guindon et al. 2010; Lanfear et al. 2017) under both the Bayesian Information Criterion (BIC) and the "greedy" algorithm (Lanfear et al. 2012) with branch lengths of alternative partitions "linked" to search for the best-fit scheme.

Phylogenetic relationships were assessed under a Bayesian inference approach using MrBayes 3.2.7 (Ronquist et al. 2012) after partitioning the data as described above. To reduce the chance of converging on a local optimum, four runs were performed. Each consisted of ten million generations and four Markov chains with default heating values. Trees were sampled every 10,000 generations. Stationarity was confirmed by plotting the –ln L per generation in the program Tracer 1.7 (Rambaut et al. 2018). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman and Rubin 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. Adequacy of mixing was assessed by examining the effective sample sizes (ESS) in Tracer, with ESS > 200 considered as satisfactory. After analyzing convergence, mixing, and sampling, the first 101 trees in the sample were discarded as "burn-in" from each run. We used the resultant 3,600 trees to calculate posterior probabilities (PP) for each bipartition on a Maximum Clade Credibility Tree in TreeAnnotator (Rambaut and Drummond 2016). Additionally, uncorrected genetic distances among species of *Enyalioides* and *Morunasaurus* were calculated in DIVEIN (Deng et al. 2010) for ND2 and are presented as an Excel file in the Suppl. material 2: Table S1.

Results

The taxonomic conclusions of this study are based on the observation of morphological features and color patterns, as well as the inferred phylogenetic relationships. This information is considered as species delimitation criteria following a general lineage or unified species concept (de Queiroz 1998; 2007).

Enyalioides feiruzae sp. nov.

http://zoobank.org/61EE1C36-C874-4742-A0BD-7FCA9478F252

Figueres 1–4A

Proposed standard English name: Feiruz wood lizards

Proposed standard Spanish name: Lagartijas de palo de Feiruz

Holotype. PERU • 1 ♂, adult; Huánuco department, Pachitea province, from the Huallaga River near Santa Rita Sur village; 9°35'33.7"S, 75°53'33.3"W, 856 m a.s.l. (above sea level); 27 Jun. 2011; P.J. Venegas leg.; CORBIDI 9316 (Fig. 1).

Paratypes. (*28*). PERU • 1 ♀, adult; same data as for holotype; CORBIDI 9317 • 1 juvenile; Huánuco department, Huánuco province, from Chaglla; 9°38'40.3"S, 75°50'57.0"W; 998 m a.s.l.; 18 Jun. 2011; P.J. Venegas leg.; CORBIDI 9315 • 1 ♂, adult, 2 juveniles; Huánuco department, Huánuco province, from a fringe of riparian forest on the left side of Huallaga River near Santa Rita Sur; 9°35'53.7"S, 75°53'21.1"W; 853 m a.s.l.; 30 Jun. 2011; P.J. Venegas leg.; CORBIDI 9314, 9318–19 • 1 ♂, 1 ♀ adults, 1 juvenile; Huánuco department, Huánuco province, Nueva Villa Paraiso (Chinchao District); 9°32'16.50"S, 76°1'1.36"W; 1,344 m a.s.l.; 01 May 2012; D. Apaza, J.C. Arredondo leg.; CORBIDI 13366, 13367, 13368 • 2 ♂, 1 ♀ adults, 1 juvenile; Huánuco department, Huánuco province, Santa Clara; 9°37'46.37"S, 75°49'49.86"W; 1,085 m a.s.l.; 21 Sep. 2014; G. Chávez, A. Beraun leg.; CORBIDI 14916,14937, 14933, 14920 • 1 ♂, adult; Huánuco department, Huánuco province, Malgotingo; 9°34'52.74"S, 75°54'12.94"W; 830 m a.s.l.; 17 Sep. 2014; D. Vásquez, A. Barboza leg.; CORBIDI 14988 • 1 juvenile; Huánuco department, Huánuco province, Malgotingo; 9°36'48.28"S, 75°57'15.32"W; 1,318 m a.s.l.; 17 Sep. 2014; D. Vásquez, A. Barboza leg.; CORBIDI 14991 • 1 juvenile; Huánuco department, Pachitea province, from Chaglla; 9°39'40.69"S, 75°50'38.30"W; 927 m a.s.l.; Aug. 2013; V. Duran, L. Lujan leg.; CORBIDI 13335 • 1 ♂, adult, 1 juvenile; Huánuco department, Leoncio Prado province, Parque Nacional Tingo María, Comunidad Campesina Tres de Mayo; 9°25'13.06"S, 75°59'33.36"W; 948 m a.s.l.; 06 Nov. 2014; G. Chávez, D. Vásquez leg.; CORBIDI 15469, 15470 • 1 ♂, 1 ♀, adults, 1 juvenile; Huánuco department, Leoncio Prado province, Quinceañera Alania; 9°22'16.82"S, 75°59'13.81"W; 1,124 m a.s.l.; 16 Nov. 2014; G. Chávez, D. Vásquez leg.; CORBIDI 15516, 15517, 15506 • 1 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°52'6.581"S, 76°28'43.994"W; 1,614 m a.s.l.; 31 March 2018; L.A. García-Ayachi leg.; CORBIDI 19544 • 1 ♂, subadult; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°51'55.503"S, 76°28'21.89"W; 1,543 m a.s.l.; 01 Apr. 2018; L.A. García-Ayachi leg.; CORBIDI 19543 • 1 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°51'31.597"S, 76°28'8.637"W; 1,520 m a.s.l.; 2 Apr. 2018; L.A. García-Ayachi leg.; CORBIDI 19545 • 2 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°47'28.039"S, 76°26'10.652"W; 1,103 m a.s.l.; 4 Apr. 2018; L.A. García-Ayachi leg.; CORBIDI 19546, 19547 • 1 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°45'51.708"S, 76°24'54.824"W; 1,071 m a.s.l.; 07

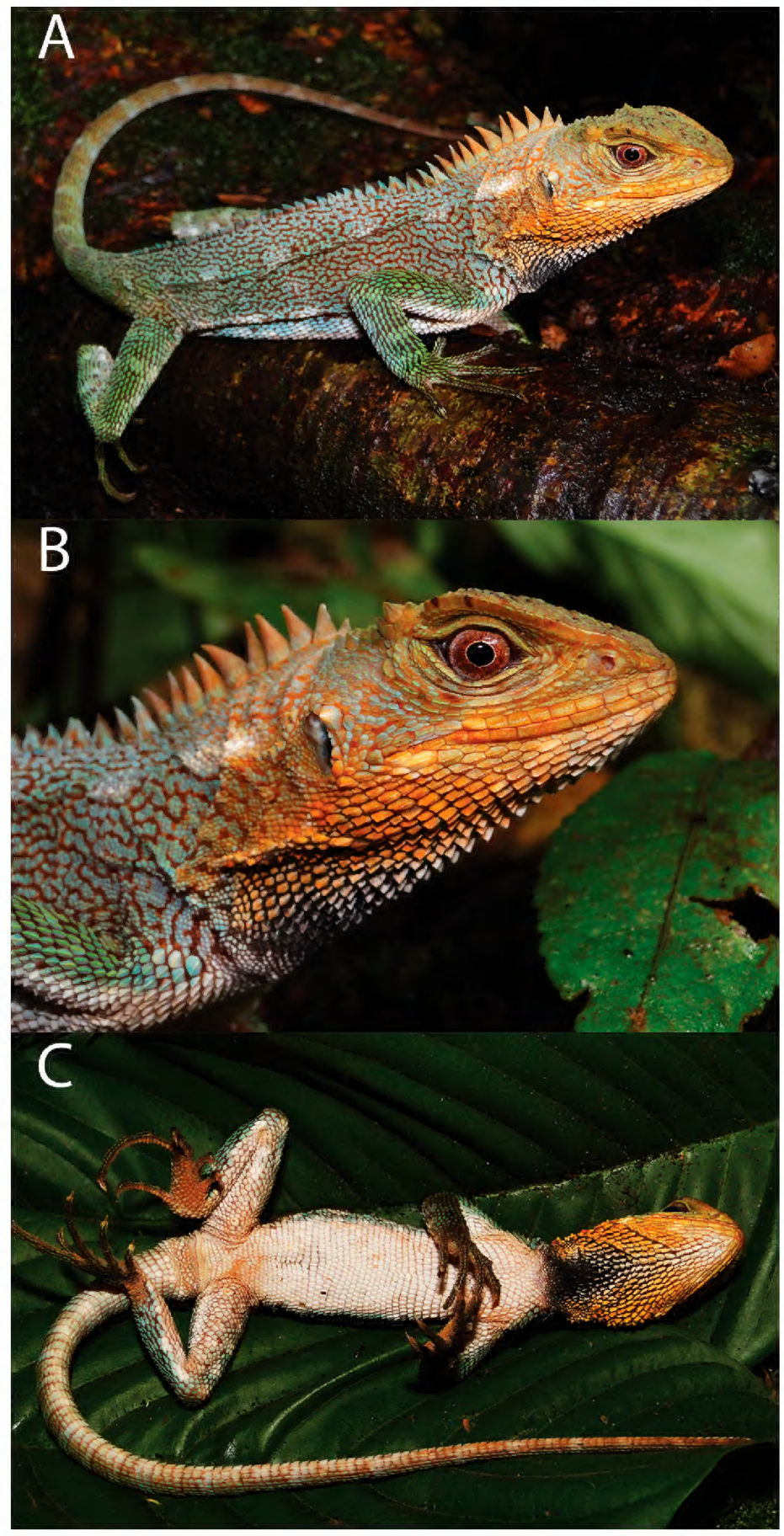

Figure 1. Holotype of *Enyalioides feiruzae* sp. nov. (CORBIDI 9316, adult male, SVL = 121 mm). (**A**) lateral view; (**B**) close-up of head; (**C**) ventral view. Photographs by P.J. Venegas.

Apr. 2018; L.A. García-Ayachi leg.; CORBIDI 19548 • 1 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°51'30.909"S, 76°28'9.845"W; 1,528 m a.s.l.; 25 Jun. 2018; L.A. García-Ayachi leg.; CORBIDI 19550 • 1 juvenile; Huánuco department, Marañón province, Nuevo Cajhán, forest on the slope of the Huamuco River; 8°48'29.799"S, 76°26'59.684"W; 1,184 m a.s.l.; 26 Jun. 2018; L.A. García-Ayachi leg.; CORBIDI 19551.

Diagnosis. *Enyalioides feiruzae* can be distinguished from other species of *Enyalioides*, except *E. binzayedi* and *E. rudolfarndti*, by the combination of the following characters (see also Table 1): (1) scales posterior to the superciliaries enlarged and pointed (relative to adjacent scales), forming a well-defined longitudinal row of distinctly raised scales across the lateral edge of the head in juveniles and adults of both sexes; (2) vertebral crest strongly projected, continuous, and decreasing in size posteriorly, with vertebrals on neck at least four times higher than those between hind limbs; (3) projecting scales on body or limbs absent; (4) ventral scales strongly keeled; (5) caudal scales heterogeneous in size on each autotomic segment; and (6) superciliary triangular flap that projects posterolaterally over each eye absent. The most similar species to *Enyalioides feiruzae* is its sister species (see below) *E. rudolfarndti* (Fig. 4B). Both species are similar in dorsal coloration, scale counts, and size; however, *E. feiruzae* differs from *E. rudolfarndti* (character states in parentheses) in having a conspicuous posteromedial black patch, rarely dark brown, in the gular region in both sexes (absent); adult males usually without an orange round blotch on the antehumeral region or a faint blotch if present (conspicuous orange blotch on antehumeral region in adult males); scales on flanks homogeneous in size (distinctly heterogeneous); and fewer supralabials 8–10, $\bar{x}$ = 9.52 (11–12, $\bar{x}$ = 11.75). The new species differs from *E. binzayedi* in having dorsal scales strongly keeled on paravertebral region and feebly keeled or smooth elsewhere (prominent medial keel on each dorsal scale); fewer supralabials 8–10, $\bar{x}$ = 9.52 (11–15, $\bar{x}$ = 12); more dorsals in transverse row between dorsolateral crests at midbody 26–39, $\bar{x}$ = 30.44 (22–31, $\bar{x}$ = 27.57); and a conspicuous posteromedial black patch in the gular region (absent).

Table 1. Summary of morphological characters and measurements (mm) of *Enyalioides binzayedi*, *E. rudolfarndti*, and *E. feiruzae* sp. n. Range (first line) and mean ± standard deviation (second line) are given for quantitative characters, except when there was no variation. Sample size between parentheses for femoral pores and maximum SVL.

Character	*E. binzayedi* *n* = 7	*E. rudolfarndti* *n* = 4	*E. feiruzae* *n* = 29
Vertebrals from occiput to base of tail	40–55 48.00 ± 5.51	42–47 45.5 ± 2.38	41–56 47.75 ± 4.00
Dorsals in transverse row between dorsolateral crests at midbody	22–31 27.57 ± 3.64	27–30 28.25 ± 1.5	26–38 31.31 ± 3.03
Ventrals in transverse row at midbody	26–32 28.14 ± 2.12	28–32 30.25 ± 3.69	25–35 29.41 ± 3.36
Transverse rows of ventrals between fore and hind limb	30–39 35.29 ± 2.81	35–38 36.75 ± 1.5	32–39 36.79 ± 2.17
Gulars	27–31 29.14 ± 1.77	33–36 34.5 ± 1.29	27–38 32.75 ± 2.60
Infralabials	10–14 11.29 ± 1.50	11 11	8–11 9.44 ± 0.68
Supralabials	11–15 12.00 ± 1.41	12–14 12.5 ± 1.29	8–11 9.72 ± 0.59
Canthals	4–6 4.43 ± 0.79	3–4 3.75	3–5 3.89 ± 0.68
Superciliaries	13–14 13.57 ± 0.53	14–18 15.25 ± 1.89	12–17 14.13 ± 1.15
Subdigitals manual digit IV	17–22 19.86 ± 1.68	19–23 20 ± 2	18–24 20.13 ± 1.82
Subdigitals pedal digit IV	24–30 27.14 ± 2.48	25–28 26.5 ± 1.29	24–32 27.93 ± 2.13
Femoral pores in males	1–2 (*n* = 2)	1 (*n* = 2)	1 (*n* = 9)
Femoral pores in females	1–3 (*n* = 5)	1 (*n* = 2)	1 (*n* = 5)
Tail length/total length	0.56–0.60 0.58 ± 0.02	0.60–1.49 0.83 ± 0.44	0.47–0.63 0.59 ± 0.03
Maximum SVL (mm) males	118 (*n* = 2)	116 (*n* = 2)	122.0 (*n* = 9)
Maximum SVL (mm) females	122 (*n* = 5)	90 (*n* = 1)	119.1 (*n* = 5)

A longitudinal row of strongly projecting scales along the lateral edge of the skull posterior and continuous with the superciliaries is also present in *Enyalioides altotambo* and *E. oshaughnessyi*, which occur west of the Andes in Ecuador and Colombia and differ from *E. feiruzae* in having smooth or slightly keeled dorsals. Additionally, *Enyalioides cofanorum* and *E. microlepis* share with the new species the presence of strongly keeled ventral scales and caudal scales of heterogeneous size on each autotomic segment. However, *E. cofanorum* differs from *E. feiruzae* (characters states in parentheses) in having a smaller body size, maximum SVL 107 mm in males and 109 mm in females (maximum SVL = 122 mm in males and 119 mm in females); scattered, projecting, large dorsal scales (absent); and a black patch covering the gular region (patch only covering the gular region posteromedially). *Enyalioides microlepis* differs from *E. feiruzae* in having more than 40 dorsal scales in a transverse line between the dorsolateral crest at midbody (38 or fewer dorsal scales); a low vertebral crest (high); and a blue gular background (white or orange).

Description of holotype. Male (Fig. 1); SVL = 121 mm; TL = 174 mm; maximum head width = 22.9 mm; head length = 21.5 mm; head height = 22.1 mm; dorsal head scales uni- or multicarinate, projected dorsally; parietal eye present; five scales immediately posterior to superciliaries conical, dorsolaterally projected, and conspicuously larger than adjacent scales; temporal scales small, pyramidal, low; one enlarged, conical pretympanic scale; superciliaries 14; canthals three; postrostrals two; supralabials nine if counted to a point below middle of eye; rostral not divided, similar in size to adjacent supralabials; lorilabials in one longitudinal row between suboculars and supralabials at level of middle of eye, and two rows anterior to this point; loreal region with small, weakly keeled, and juxtaposed scales; nasal at level of supralabial III; infralabials nine if counted to a point below middle of eye; mental (2.48 mm wide × 1.51 mm high) wider and 1.5 times higher than adjacent infralabials; postmentals two; gulars ventrally projected, compressed laterally and

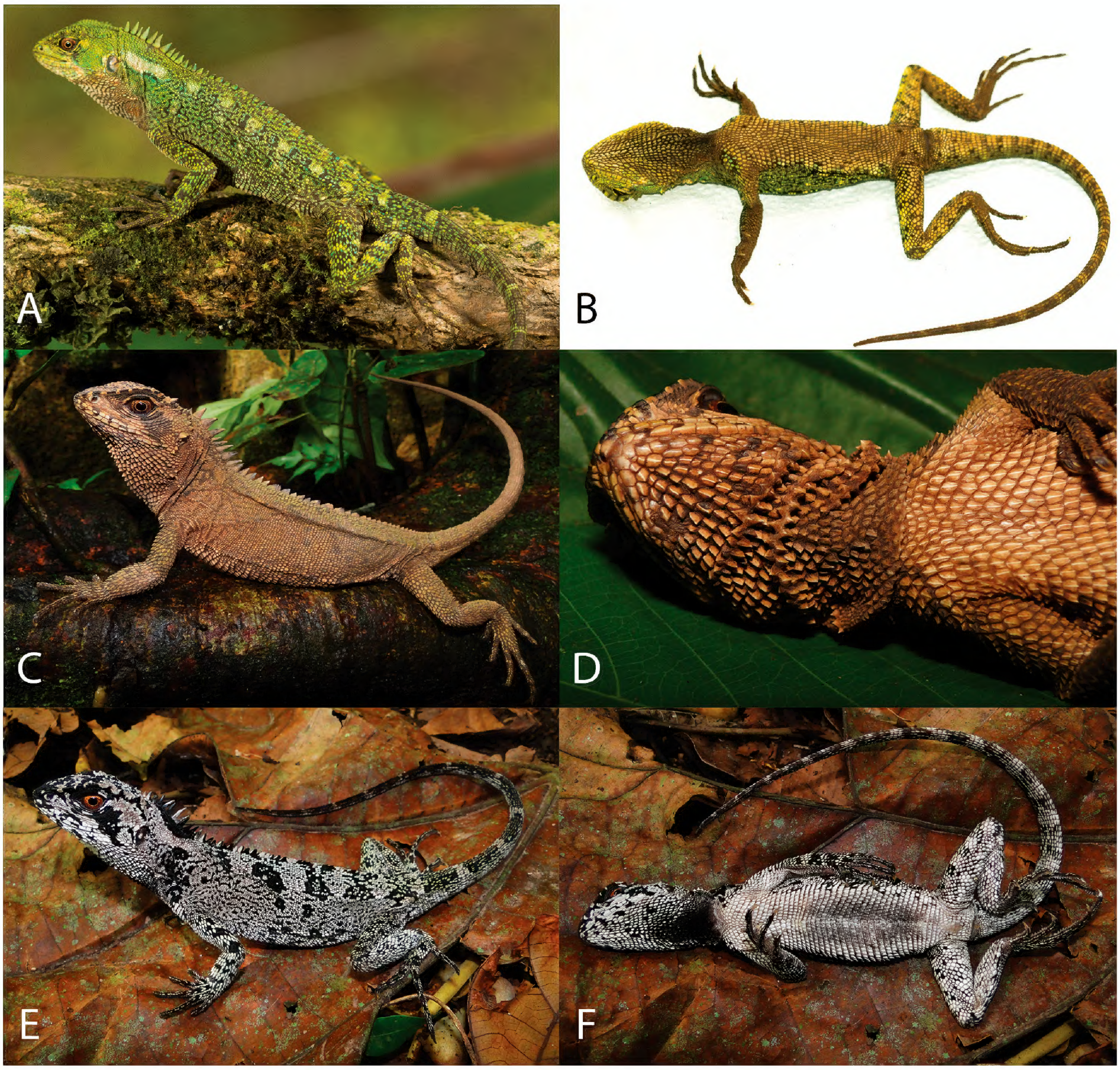

Figure 2. Adult specimens of *Enyalioides feiruzae* sp. nov. Male (**A**, **B**, CORBIDI 15469), female (**C**, **D**, CORBIDI 9317), male (**E, F,** CORBIDI 9314). Photographs (**A**, **B**) by G. Chávez and (**C–F**) by P.J. Venegas.

separated from each other by black skin covered with tiny granular scales; gular fold complete midventrally, extending dorsally and posteriorly to form an antehumeral fold; neck with some oblique folds, and a dorsolateral row of enlarged scales; ventral end of oblique fold immediately anterior to antehumeral fold with approximately five enlarged scales similar in size to adjacent gulars, but more than three or four times the size of adjacent fold scales.

Vertebral crest strongly projected and decreasing in size posteriorly, with vertebrals on neck at least four times higher than those between hind limbs; crest bifurcates at a point approximately 15 mm posterior to the cloaca, and extends onto tail about 1/3 its length; body flanks between fore and hind limbs with slight dorsolateral and ventrolateral folds, as well as oblique folds; scales on dorsolateral folds strongly keeled, slightly larger than adjacent scales; dorsal scales in paravertebral region enlarged, strongly keeled, and mucronate, decreasing in size as they approach the dorsolateral fold; scales on flanks slightly smaller than dorsals, keeled or smooth, nearly homogeneous in size except for some scattered enlarged keeled scales near both the ventrolateral region and the groins; ventral scales imbricate, strongly keeled, rectangular or rhomboid, with a posteromedial mucron; ventrals more than twice the size of dorsals.

Limb scales strongly keeled dorsally and keeled or feebly keeled ventrally; scales on dorsal aspect of thighs more or less homogeneous in size; scales on posterior aspect of thighs strongly heterogeneous in size, with most scales less than half the size of those scales on anterior and ventral aspects; subdigitals on finger IV 21; subdigitals on toe IV 27; one femoral pore on each side; tail laterally compressed and gradually tapering posteriorly; caudal scales keeled at the base of tail, becoming strongly keeled and imbricate towards tip, gradually increasing in size posteriorly on lateral and dorsal aspects of each

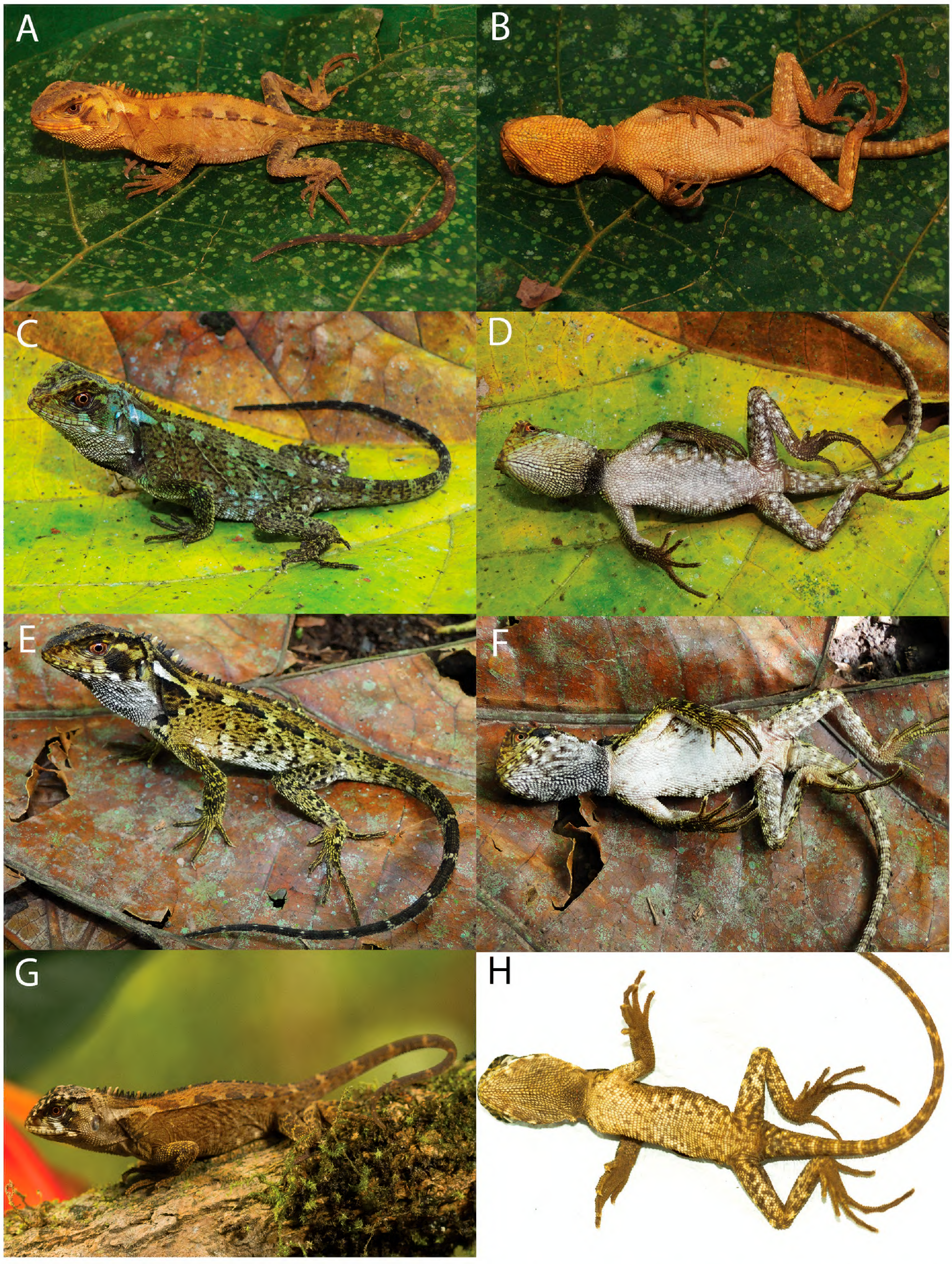

Figure 3. Juvenile specimens of *Enyalioides feiruzae* sp. nov. (**A**, **B**) CORBIDI 9315, (**C**, **D**) CORBIDI 9318, (**E**, **F**) CORBIDI 9319, (**G**, **H**) CORBIDI 15470. Photographs (**A–F**) by P.J. Venegas and (**G**, **H**) by G. Chávez.

caudal segment; caudals larger ventrally than dorsally; individual caudal segments three scales long ventrally and five scales long dorsally.

Color in life of holotype (Fig. 1): Dorsal surface of body, limbs and tail turquoise; dorsal surface of head with a greenish tone and scattered dark brown flecks; side of

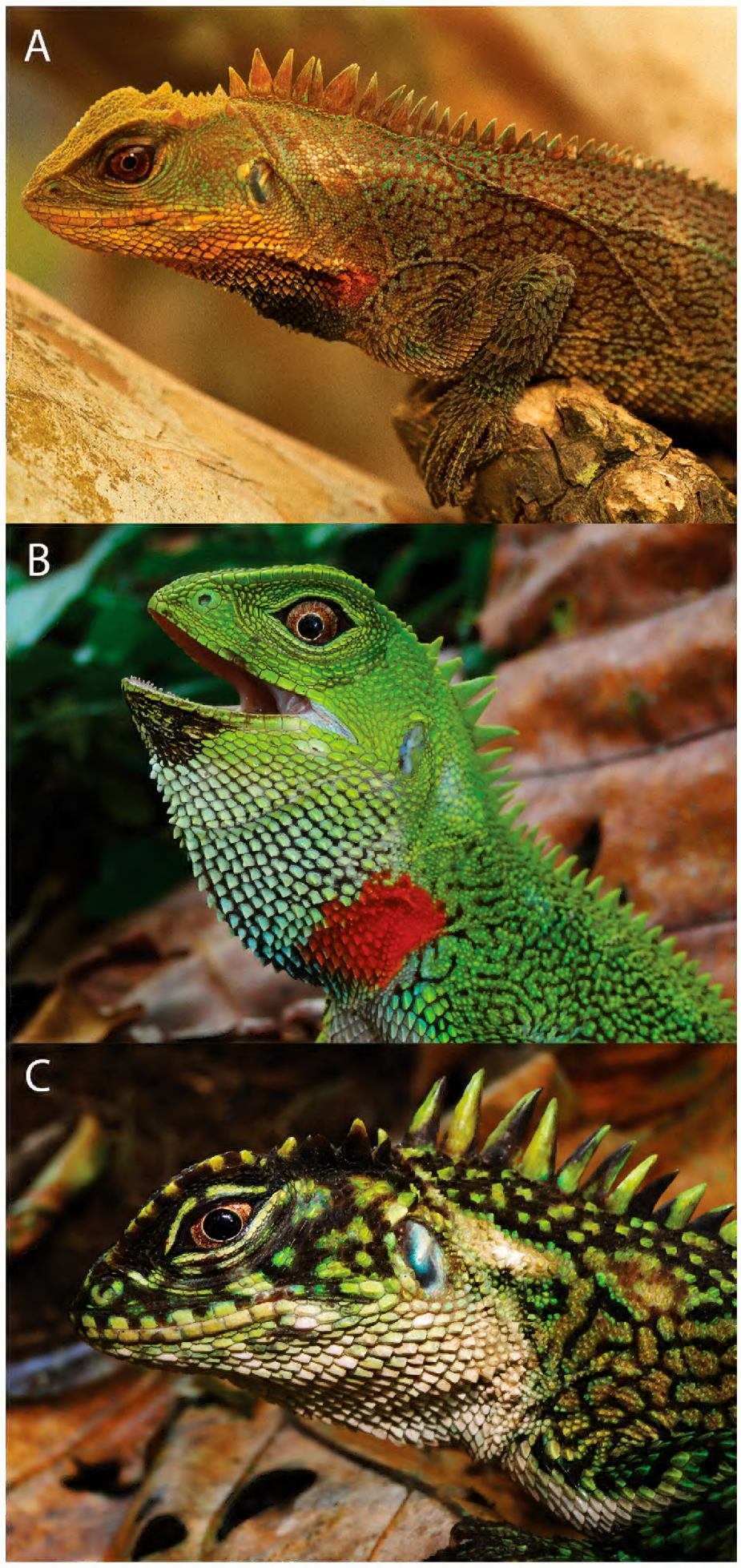

Figure 4. Head and anterior body region in lateral view of adult male specimens of *Enyalioides feiruzae* sp. nov. (**A**, CORBIDI 14916, paratype), *E. rudolfarndti* (**B**, CORBIDI 7209, holotype), and *E. binzayedi* (**C**, CORBIDI 8828, holotype). Photographs (**A**) by G. Chávez and (**B**, **C**) by P.J. Venegas.

head orange on nasal, loreal, ocular, labial and mandibular regions; orange reticulation in temporal region and dorsal surface of neck; sides of neck with reddish brown reticulation and a faint postympanic white stripe; vertebral crest orange on the neck and turquoise with a reddish-brown base elsewhere; dorsum with a dorsolateral row of faint pale blotches and covered by reddish brown reticulations that are more defined on the flanks; limbs and tail with a greenish tone; limbs with dark brown or nearly black marks and flecks; chin white; throat orange with a black patch posteriorly; chest, venter, ventral surface of limbs and tail white with faint marks on ventral surface of thighs; iris reddish brown, darker in the center than peripherally, with a golden ring bordering the pupil.

Color in ethanol 70%: Dorsal surface of body, head, limbs and tail grayish turquoise; dorsal surface of head and sides of head with a dusty brown tone and dark brown flecks; labials gray; dorsal surface of neck with a dusty brown tone, sides of neck with dark reticulations and a faint white postympanic stripe; vertebral scales on neck with dusty brown tips; dorsum with dark reticulations; tail with a dusty brown tone; dorsal surface of limbs with dark flecks and marks, more abundant on hind limbs; chin and throat cream, covered by a black patch on the posteromedial gular region and ventral surface of neck; chest, belly, ventral surface of limbs and tail dirty cream with faint marks on ventral surface of thighs.

Intraspecific variation. Meristic and morphometric characters of *Enyalioides feiruzae* are summarized in Table 1. Scales on flanks are keeled, nearly homogeneous in size, slightly smaller or similar to dorsals in all specimens, but some individuals have a few scattered, enlarged scales near the insertion of hind limbs or along the ventrolateral region. Caudal segments are 5–6 scales long laterally. Color of the iris is nearly identical in all specimens, varying only from brown to reddish brown, darker in the center, with a golden ring bordering the pupil. *Enyalioides feiruzae* is a polymorphic species with more variation in color in males and juveniles than in adult females (Figs 2, 3). The dorsal background of adult males can be brownish turquoise (CORBIDI 14916) (Fig. 4A), gray or greenish brown with pale (CORBIDI 13366) or black (CORBIDI 9314; Fig. 2E) transverse bands along dorsum. The orange head coloration of the holotype is restricted to the labials and throat of other adult males. An adult male specimen (CORBIDI 14916) has two inconspicuous pale orange blotches, one on each side of the ventrolateral region of neck (Fig. 4A). One subadult male (CORBIDI 15469, SVL = 98.8 mm) has the dorsal background light green sprinkled with sky blue flecks; short pale transverse bands along dorsum and black reticulations on dorsum and flanks; dorsal surface of limbs with black flecks and transverse bands; tail with dark brown or black marks; chin gray and throat grayish brown, ventral surface of neck up to the neck fold dark; chest, venter, ventral surface of limbs and tail tan white with dark brown flecks on belly, thighs and tail (Fig. 2A, B). Ventrally, specimen CORBIDI 9314 (Fig. 2F) has a white throat with black flecks, and a black patch posteromedially; the chest, venter, ventral surface of limbs and tail are white with a large grayish patch along the belly and black flecks on the ventral surface of thighs and base of tail.

Among adult females (Fig. 2), the dorsal background is greenish brown (CORBIDI 14933) or floury brown (CORBIDI 9317; Fig. 2C), with faint dark brown (CORBIDI 14933), transverse bars (dorsum, limbs, and tail) or blotches (flanks); some specimens have dark subocular (broad) and supratemporal (narrow) stripes, whereas others have a faint postympanic stripe. Specimen CORBIDI 14933 has a distinct pale subocular stripe and a white blotch on rictal region. Specimen CORBIDI 14933 has a cinnamon brown venter without a dark patch, while specimen CORBIDI 9317 has a brown throat with dark brown

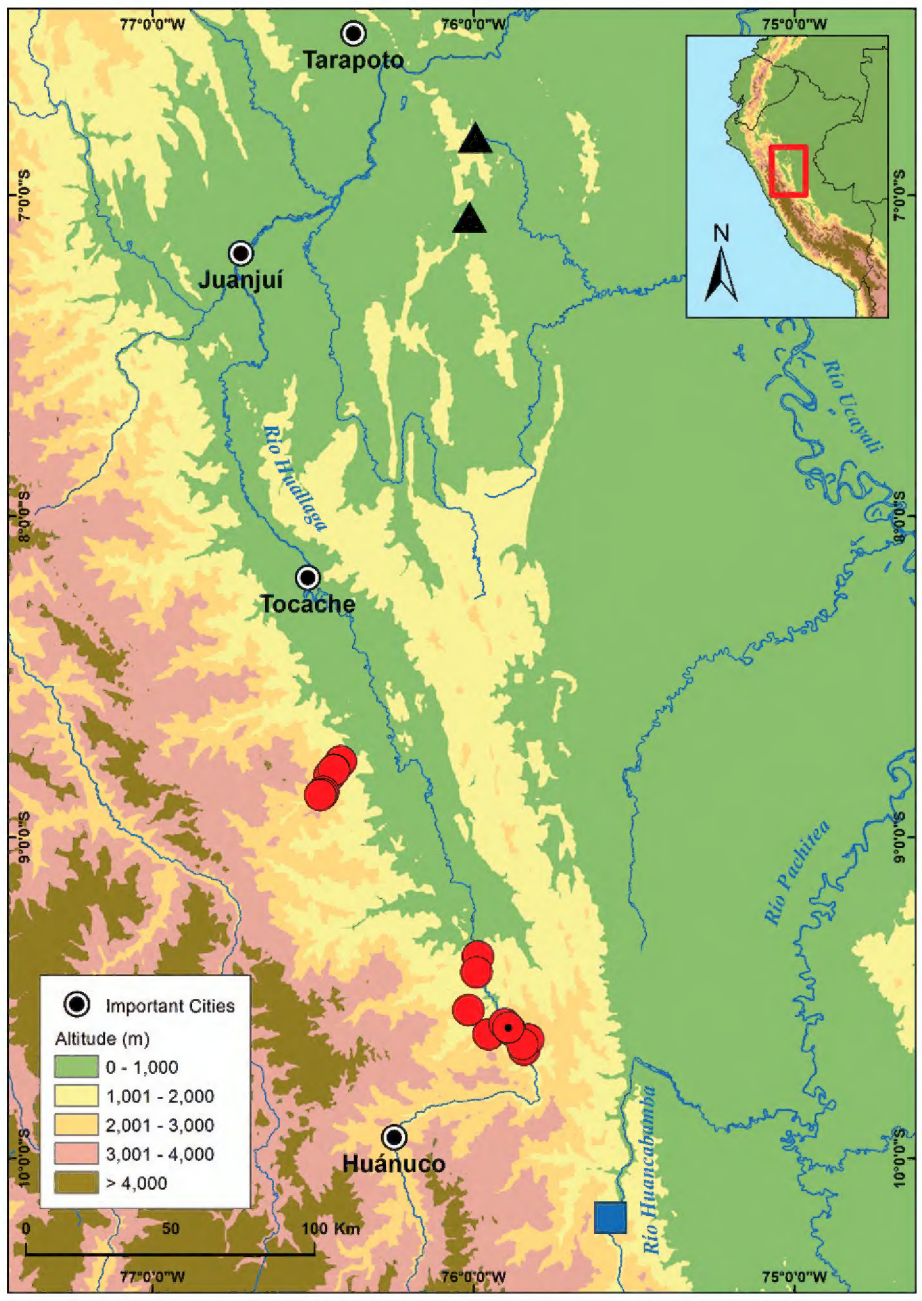

Figure 5. Distribution of *Enyalioides binzayedi* (triangles), *E. feiruzae* sp. nov. (circles), and *E. rudolfarndti* (squares) in Peru.

flecks and a dark brown patch posteromedially (Fig. 2D), and a tan venter with scattered dark brown flecks on belly and dark brown marks on ventral surface of thighs.

Dorsal background in juveniles varies among different tones of brown and green (Fig. 3), with a paravertebral row of either dark brown blotches with pale interspaces (CORBIDI 9315, 9319 and 15470) or pale blotches (CORBIDI 9318). Flanks can have small pale blotches and black flecks (CORBIDI 9318), transverse rows of dark brown (nearly black) blotches and dark brown flecks (CORBIDI 15506), or faint transverse cream bands and dark brown marks (CORBIDI 9319). All juvenile specimens have dark marks or flecks on head, dark supratemporal stripe and postocular blotch, and postympanic pale stripe. Ventrally, CORBIDI 9315 is immaculate tan without a dark patch on gular region (Fig. 3B). Other specimens are grayish white, dirty white or white ventrally (CORBIDI 9318–19, 15470), with dark or faint brown marks and flecks on throat, belly and ventral surface of thighs and a dark brown or gray patch on the ventral surface of neck (Fig. 3D, F & H). Sexual dichromatism is not obvious in the dorsal background coloration due to the high variation presented in both sexes. The turquoise hue in the dorsum of some adult males is absent in the examined females. However, the orange coloration in the head and throat of some adult males, and the black patch on the posterior half of throat is absent in females.

Distribution and natural history observations. *Enyalioides feiruzae* is known from the Huallaga River basin (Huánuco Department) on the Amazonian slope of the Andes of central Peru at elevations between 830–1,614 m a. s. l. Specimens from Pachitea and Huánuco provinces were collected in patches of secondary forest surrounded by pasturelands and coffee, corn or fruit plantations, whereas specimens from Tingo María National Park in Leoncio Prado province were found in a steep primary forest area.

The general landscape along the Huallaga River basin between the Huánuco and Pachitea provinces consists of steep areas, which are impacted by human activities like agriculture and cattle ranching, with scattered patches of secondary forest and narrow fringes of riverine forest. In contrast, Tingo María National Park is an area of primary forest, where the ground is covered by leaf litter, fallen trunks and rocks. Streams with small, torrential waterfalls are common. Vegetation includes lichens, ferns, orchids, epiphytes, bushes, and trees. All localities where *Enyalioides feiruzae* was collected lie within Peruvian Yungas (Olson et al. 2001).

Most individuals reported here were collected at night sleeping on vertical and horizontal stems of bushes 20–150 cm above the ground. One juvenile was found sleeping in the middle of a big leaf 30 cm above the ground. Another juvenile was found sleeping in a vertical stem, and when disturbed by the light of the headlamp, it dropped and ran to hide in a burrow under a big rock. Male CORBIDI 14916 was found at night sleeping on branches in a small patch of secondary forest surrounded by crops. Adults from Tingo María National Park were caught sleeping vertically on stems near streams and waterfalls; male CORBIDI 15516 was found 1.5 meters away from female CORBIDI 15517, both sleeping vertically.

Etymology. The specific name is a noun in the genitive case and is a patronym for Feiruz, a female green iguana, muse and lifelong friend, owned by Catherine Thomson from Farmington Hills, Michigan, USA, who supported our taxonomic research and nature conservation through the BIOPAT initiative.

Phylogenetic relationships. Selected partitions and models were (i) tRNAs + 1st and 2nd codon positions of ND1, ND2 and COI [GTR+I+G]; (ii) 3rd codon position of ND1, ND2 and COI [GTR+I+G]. In agreement with previous hypotheses (Torres-Carvajal and de Queiroz 2009), species of *Enyalioides* were recovered in two clades, one containing *E. heterolepis* and *E. laticeps*, and the other including all remaining species of *Enyalioides* (N = 14), as well as *Morunasaurus annularis* and *M. peruvianus* (Fig. 6). *Enyalioides feiruzae* (N = 4) is strongly supported (PP = 1) as monophyletic and sister to *E. rudolfarndti* (N = 3). They form a maximally supported clade with (in branching order) *E. binzayedi*, *E. sophiarothschildae*, *E. palpebralis*, and *E. azulae*.

Interspecific mean genetic p-distances for the ND2 gene (Suppl. material 2: Table S1) ranged from 0.023 (*Enyalioides feiruzae*/*E. rudolfarndti*) to 0.269 (*E. altotambo*/*E. laticeps*). The second lowest distance was 0.031 (*E. microlepis*/*E. cofanorum*).

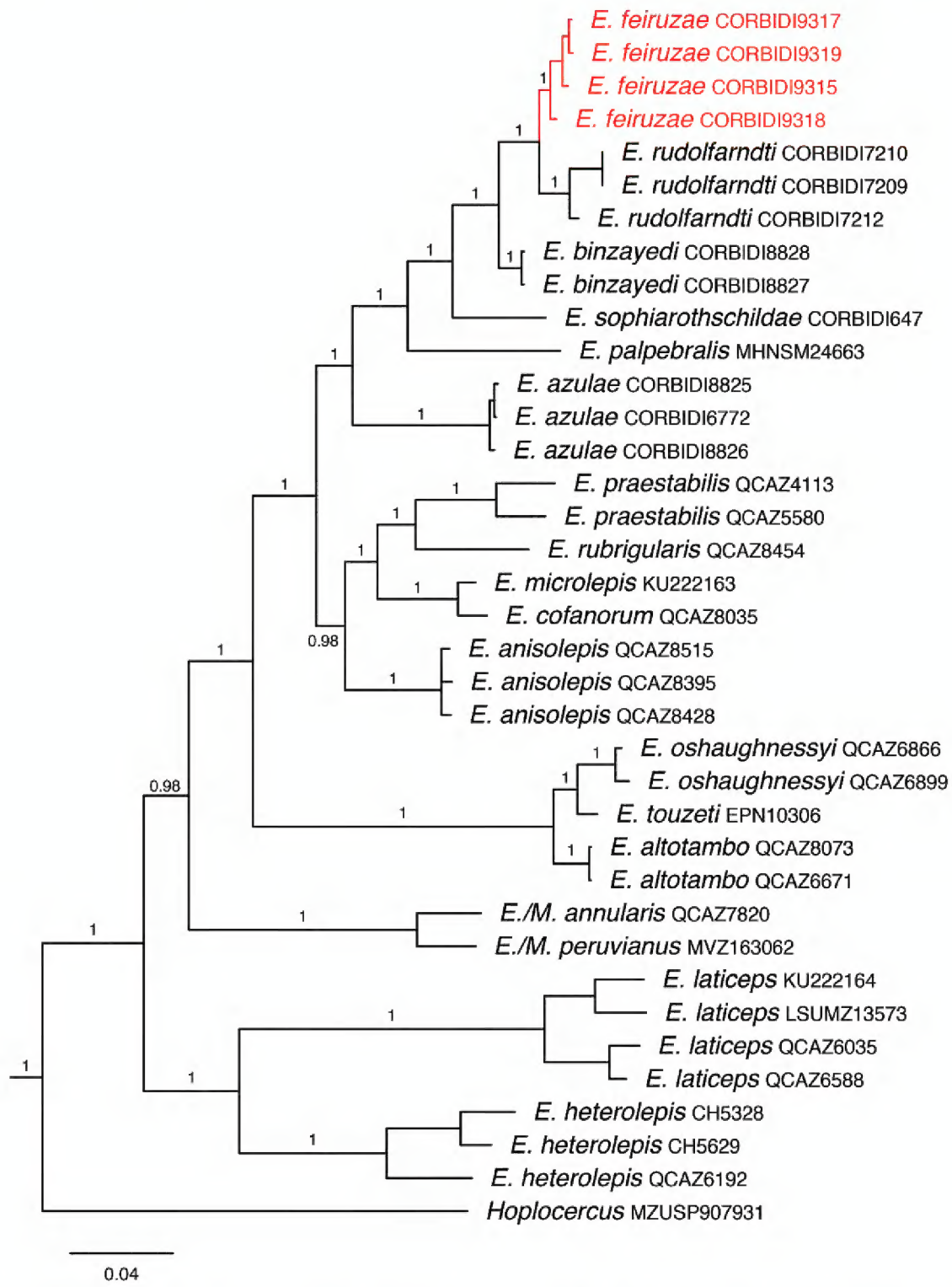

Figure 6. Phylogeny of Hoplocercinae. Maximum clade credibility tree based on a Bayesian analysis of mtDNA sequences. Posterior probabilities are indicated next to branches, except for short "intraspecific" branches (not shown for clarity). The new species described in this paper is shown in red. Outgroup taxa are not shown.

Discussion

The phylogenetic tree presented here supports the position of the new species within the clade (*E. azulae* (*E. palpebralis* (*E. sophiarothschildae* (*E. binzayedi* (*E. rudolfarndti*, *E. feiruzae* sp. nov.))))), herein named "*palpebralis* group", with maximal support (Fig. 6). Species in this clade occur mostly along the Amazonian slopes of the Andes in Peru and, except for *E. palpebralis*, were discovered in the last decade (Venegas et al. 2011; Venegas et al. 2013b; Torres-Carvajal et al. 2015). Curiously, the lining of the throat in all species of this clade is black or dark purple, which in some cases extends to the floor of the mouth. Moreover, the lining of the mouth in some adult males of *E. palpebralis* is bright orange (Torres-Carvajal et al. 2011). Dark pigment on lining of throat or mouth is absent in *E. anisolepis*, *E. heterolepis*, *E. laticeps*, *E. microlepis*, *E. oshaughnessyi*, *E. praestabilis*, *E. rubrigularis* and *E. touzeti*; this condition has not been examined in other species of hoplocercines. This suggests that presence of dark pigment in the buccal mucosa is a synapomorphy of the "*palpebralis* group".

The current landscape of the Huallaga River basin is the result of tectonic activity and climatic oscillations that occurred from the Late Oligocene to the Early Miocene (Brown and Twomey 2009; Mora et al. 2010; Gonzales and Pfiffner 2012; Pfiffner and Gonzales 2013). Mountain uplifting and cooling periods have been pointed as key drivers of vicariance events and subsequent allopatric speciation in the central Andes, where species of the "*palpebralis* group" occur (Winger and Bates 2015; Lagomarsino et al. 2016, Wollenberg-Valero et al. 2019). As in other Andean sister species (Roberts et al. 2006; Brown and Twomey 2009, Winger and Bates 2015; Winger 2017), vicariance is probably the main cause leading to the divergence between *E. feiruzae* and its sister species *E. rudolfarndti*. We acknowledge that the ND2 genetic distance between *E. feiruzae* and *E. rudolfarndti* is the lowest among species of *Enyalioides* (see Suppl. material 2: Table S1); however, we believe that differences in key color features (throat patch, antehumeral blotch) that are presumably used for species recognition represent strong evidence for assigning both taxa to different species.

The upper basin of the Huallaga River has been highly disturbed by agriculture activities (Catenazzi and von May 2014). In fact, specimens of *E. feiruzae* were collected mostly in fragmented habitats surrounded by cacao and corn plantations. The only known protected populations are those from Tingo María National Park. On the basis of our limited knowledge on distribution, population status, and the resilience of *E. feiruzae* in a fragmented landscape, we recommend to place *E. feiruzae* in the Data Deficient category of the IUCN Red List of Threatened species (IUCN 2019).

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Supplementary material 1

Material examined

Authors: Pablo J. Venegas, Germán Chávez, Luis A. García-Ayachi, Vilma Duran, Omar Torres-Carvajal

Data type: note

Explanation note: Collection data for Museum specimens examined in the morphological comparisons. The specimens come from the herpetological collection of Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru, and the reptile collection of the Zoological Museum (QCAZ), Pontificia Universidad Católica del Ecuador in Quito, Ecuador.

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Link: https://doi.org/10.3897/evolsyst.5.69227.suppl1

Supplementary material 2

Table S1

Authors: Pablo J. Venegas, Germán Chávez, Luis A. García-Ayachi, Vilma Duran, Omar Torres-Carvajal

Data type: excel table

Explanation note: Uncorrected *p*-distances for the ND2 gene region between species of Hoplocercinae.

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